

Chaotic attractors in the four-dimensional Leslie-Gower competition model

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Abstract

We study the occurrence of the chaotic attractor in the four-dimensional classical Leslie-Gower competition model. We find that chaos can be generated by a cascade of quasiperiod-doubling bifurcations starting from a supercritical Neimark-Sacker bifurcation of the positive fixed point in this model. The chaotic attractor is contained in the three-dimensional carrying simplex, that is a globally attracting invariant manifold. Biologically, the result implies that the invasion attempts by an invader into a trimorphic population under the Leslie-Gower dynamics can lead to chaos.

Keywords: Leslie-Gower model, carrying simplex, chaotic attractor, quasiperiod-doubling cascades, invasion

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1. Introduction

Consider the discrete-time dynamical system modelling the interaction of n species induced by the map of Kolmogorov type

$$T(x) = (x_1 F_1(x), \dots, x_n F_n(x)), \quad x \in \mathbb{R}_+^n := [0, \infty)^n, \quad (1)$$

where F_i are continuous with $F_i(x) > 0$ for all $x \in \mathbb{R}_+^n$, $i = 1, \dots, n$. Here, x denotes the vector of populations at one generation, and $T(x)$ is the corresponding vector at the next generation. The map T is called a competitive map in a subset $W \subset \mathbb{R}_+^n$ if for all $x, y \in W$ such that $T_i(x) \leq T_i(y)$ for all $i = 1, \dots, n$ but $T(x) \neq T(y)$ one has that

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8 $x_i < y_i$ provided $y_i > 0$. Since the early work of Hirsch [1] and Smith [2], it is well
9 known that most competitive maps admit an invariant hypersurface Σ of codimension
10 one, known as the carrying simplex, which attracts all nontrivial orbits (see, for instance,
11 [3, 4, 5, 6, 7, 8, 9]). The origin 0 is a repeller for T , and Σ is the boundary in \mathbb{R}_+^n of the
12 basin of repulsion of the origin which satisfies the following properties:

- 13 (P1) Σ is compact and unordered, i.e. if $x, y \in \Sigma$ such that $x - y \in \mathbb{R}_+^n$, then $x = y$;
- 14 (P2) Σ is homeomorphic via radial projection to the $(n - 1)$ -dimensional standard prob-
15 ability simplex $\Delta^{n-1} = \{x \in \mathbb{R}_+^n : \sum_{i=1}^n x_i = 1\}$;
- 16 (P3) $\forall x \in \mathbb{R}_+^n \setminus \{0\}$, there exists some $y \in \Sigma$ such that $\lim_{k \rightarrow \infty} |T^k(x) - T^k(y)| = 0$;
- 17 (P4) $T(\Sigma) = \Sigma$, and $T : \Sigma \mapsto \Sigma$ is a homeomorphism.

18 In particular, the classical discrete-time models admitting a carrying simplex include the
19 Leslie-Gower model (see [9])

$$T_i(x) = \frac{(1 + r_i)x_i}{1 + \sum_{j=1}^n b_{ij}x_j}, \quad r_i, b_{ij} > 0, \quad i, j = 1, \dots, n, \quad (2)$$

20 the Atkinson-Allen model (see [10])

$$T_i(x) = \frac{(1 + r_i)(1 - a_i)x_i}{1 + \sum_{j=1}^n b_{ij}x_j} + a_i x_i, \quad 0 < a_i < 1, r_i, b_{ij} > 0, \quad i, j = 1, \dots, n, \quad (3)$$

21 and the Ricker model (under mild conditions) (see [5, 6, 8])

$$T_i(x) = x_i \exp(r_i(1 - \sum_{j=1}^n b_{ij}x_j)), \quad r_i, b_{ij} > 0, \quad i, j = 1, \dots, n. \quad (4)$$

22 The importance of the existence of a carrying simplex stems from the fact that it
23 contains all the interesting dynamics, such as the periodic orbits, quasiperiodic orbits and
24 heteroclinic cycles. For 1D (i.e. $n = 1$) competitive maps admitting a carrying simplex,
25 there is a globally attracting positive fixed point as the carrying simplex, so the dynamics
26 is trivial. For 2D competitive maps admitting a carrying simplex, every trajectory also
27 converges to a fixed point (see [11]), because the map restricted to the one-dimensional
28 carrying simplex is a homeomorphism. For 3D competitive maps admitting a carrying
29 simplex, nontrivial dynamics such as Neimark-Sacker bifurcations and heteroclinic cycles
30 can occur (see, for example, [8, 9, 10, 11, 12]). Neimark-Sacker bifurcation is the birth

of an invariant cycle from a fixed point in discrete-time systems, and either all orbits are periodic, or all orbits are dense on the invariant cycle (in this case, it is called a quasiperiodic curve). However, it was proved in [6] and [13] that only trivial dynamics can occur, that is every orbit converges to a fixed point, when there is no positive fixed point or there is a unique positive fixed point whose index is -1 by the topological results on homeomorphisms of the plane. Criteria on the global stability of the positive fixed point are provided in [14] and [15].

The 2D Leslie-Gower model (2) was studied by Liu and Elaydi [16] and Cushing *et al.* [17] in detail, which has the same dynamic scenarios as the (2D, i.e. $n = 2$) Lotka-Volterra competition model

$$\frac{dx_i(t)}{dt} = x_i(t)(\beta_i - \sum_{j=1}^n \alpha_{ij}x_j(t)), \quad \beta_i, \alpha_{ij} > 0, \quad i, j = 1, \dots, n. \quad (5)$$

In [9], Jiang and Niu studied the 3D Leslie-Gower model (2), which was classified into 33 stable equivalence classes in terms of inequalities on the parameters r_i and b_{ij} via the boundary dynamics on the 2D carrying simplex. In classes 26 – 31, Neimark-Sacker bifurcations can occur, while in classes 1 – 25 and 33, every nontrivial trajectory converges to a fixed point on the carrying simplex. Their results show that the 3D Leslie-Gower model (2) also has the similar dynamic scenarios as the 3D Lotka-Volterra competition model (5) (see [18, 19]). The reader can consult, for instance, [20, 21, 22, 23, 24, 25, 26, 27], for more results on the Lotka-Volterra competition model (5).

It is known that chaos cannot occur in the 3D competitive Lotka-Volterra model (5) by Hirsch's carrying simplex theory for competitive continuous flow in [1] and the Poincaré-Bendixson theorem for planar continuous flow. However, though the Leslie-Gower model (2) has a carrying simplex, it can not guarantee that there is no chaos in the 3D Leslie-Gower model (2) since the Poincaré-Bendixson theorem does not hold for discrete-time systems. The results in [9, 13] seem to imply that the chaos may not occur in the 3D Leslie-Gower model (2). On the other hand, we have carried out a brute-force numerical search to try to find the possible parameters such that the orbit of the Leslie-Gower model behaves chaotic, but failed. Such numerical search has also been employed for the 3D Atkinson-Allen model (3) and the Ricker model admitting a carrying simplex (4), but we have not find any chaotic behavior. Moreover, we have also

60 carried out lots of numerical simulations for the Poincaré map of the three-dimensional
 61 periodic Lotka-Volterra competition model [5], that is the positive parameters β_i, α_{ij} in
 62 (5) are time-periodic with the same period, which also admits a carrying simplex by [3, 5].
 63 Periodic orbits and quasiperiodic curves, corresponding to subharmonic and quasiperiodic
 64 solutions of the periodic Lotka-Volterra model, were detected for the Poincaré map, but
 65 the chaotic attractor has not been found. It seems to us that there might be no chaos
 66 in these classical 3D competitive discrete-time systems admitting a carrying simplex
 67 by our numerical experiments and the results in [9, 10, 13, 18] comparing with the 3D
 68 competitive continuous-time systems (see [18, 19, 28] for example). Therefore, we turn to
 69 explore the occurrence of chaos in the 4D classical discrete-time models, and we find that
 70 the chaotic attractor can occur in the Leslie-Gower model (2) of four mutually competing
 71 species.

72 Specifically, consider the 4D Leslie-Gower competition model T given by

$$T_i(x) = \frac{(1 + r_i)x_i}{1 + \sum_{j=1}^4 r_i a_{ij} x_j}, \quad r_i, a_{ij} > 0, \quad i, j = 1, 2, 3, 4 \quad (6)$$

73 with

$$r_i = [0.08, \mu, 0.15, 0.28], \quad (7)$$

74 and

$$a_{ij} = \begin{bmatrix} 2.58 & 4.25 & 3.72 & 0.085 \\ 7.3 & 2.75 & 0.01 & 1.82 \\ 0.074 & 1.19 & 3.32 & 4.64 \\ 3.8 & 1.08 & 1.7 & 3.64 \end{bmatrix}, \quad (8)$$

75 where $\mu > 0$ is a free parameter. We find that chaos can occur in this Leslie-Gower model
 76 of four competing species for some μ . For example, when $\mu = 0.36$, a chaotic attractor
 77 is detected which is shown in Fig. 1. The corresponding Lyapunov exponents which can
 78 be computed by using MatContM [29, 30] based on the QR method (see [31, 32]) are
 79 0.0011, 0, -0.0463 and -0.1751 , which implies a Lyapunov dimension (see [31, 33]) of
 80 2.024. This means that the invertible bounded 4D Leslie-Gower map of type (2) can has
 81 a 3D carrying simplex containing a chaotic attractor.

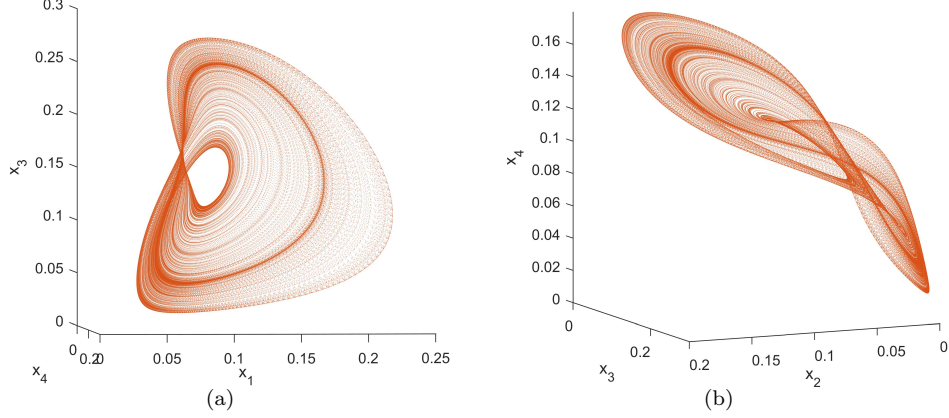


Figure 1: A chaotic attractor occurs at $\mu = 0.36$. (a) The projection of the chaotic attractor on the $x_1x_3x_4$ space. (b) The projection of the chaotic attractor on the $x_2x_3x_4$ space.

2. Derivation of the Leslie-Gower model

In this section, we give a mechanistic derivation of the Leslie-Gower model induced by the map (2) from first principles.

We assume that the season is divided into two periods: one of competition and one of reproduction. During the first period, the individuals of n species do not die, but compete for n different resources R_j , $j = 1, \dots, n$. Assuming chemostat dynamics of the resources and a Holling type I functional response, we obtain the following system of ordinary differential equations for the resource dynamics:

$$\frac{dR_i}{dt} = D_i(\bar{R}_i - R_i) - R_i \sum_{j=1}^n a_{ij}x_j, \quad i = 1, \dots, n. \quad (9)$$

Assuming the resource dynamics is fast, the resource concentrations will have reached the following steady state by the end of the period of competition:

$$R_i = \frac{\bar{R}_i}{1 + \sum_{j=1}^n \frac{a_{ij}}{D_i} x_j}, \quad i = 1, \dots, n. \quad (10)$$

During the period of reproduction, individuals of species i will use only the resource R_i given by (10) to produce offspring (with a conversion factor γ_i) born at the beginning of the next period of competition and then die. Putting all these assumptions together, we finally arrive at the following map T taking the state of the community at the beginning

of one period of competition to the next one:

$$T_i(x) = \frac{\gamma_i \bar{R}_i x_i}{1 + \sum_{j=1}^n \frac{a_{ij}}{D_i} x_j}, \quad i = 1, \dots, n, \quad (11)$$

which is, of course, exactly the map (2), but with the parameters denoted in a different way. In this paper we mainly discuss the occurrence of the chaos and the route to chaos in the Leslie-Gower model of four competing species, so we shall keep the parameters of (6) to make comparison with the similar models treated in the papers mentioned above easier.

3. Preliminaries

Let $\dot{\mathbb{R}}_+^n = \{x \in \mathbb{R}_+^n : x_i > 0, i = 1, \dots, n\}$ be the open positive cone and $\pi_i = \{x \in \mathbb{R}_+^n : x_i = 0\}$ be the i th coordinate plane. Let $\dot{\Sigma} = \Sigma \cap \dot{\mathbb{R}}_+^n$ denote the interior of the carrying simplex Σ and $\partial\Sigma = \Sigma \setminus \dot{\Sigma}$ denote the boundary of Σ .

Lemma 1 (see [9, Corollary 3.1]). *Any n -dimensional Leslie-Gower model (2) has a $(n - 1)$ -dimensional carrying simplex Σ satisfying the properties (P1)–(P4) in section 1.*

Lemma 1 implies that the long-term behavior of the Leslie-Gower model (2) is determined by the dynamics on Σ , and the nonzero forward limit sets in \mathbb{R}_+^n all lie on Σ . In particular, for the 4D Leslie-Gower model T given by (6), it has a 3D carrying simplex Σ which is homeomorphic to the tetrahedron Δ^3 (see Fig. (4)). Note that each coordinate plane π_i is positively invariant under T , and $T|_{\pi_i}$ is a 3D Leslie-Gower model which has a 2D carrying simplex homeomorphic to the triangle Δ^2 , where $T|_{\pi_i}$ is the restriction of T to π_i . Moreover, the boundary of Σ for T is composed of the 2D carrying simplices of $T|_{\pi_i}$, i.e. $\partial\Sigma = \cup_{i=1}^4 (\partial\Sigma)_i$, where $(\partial\Sigma)_i = \partial\Sigma \cap \pi_i$ is the carrying simplex of $T|_{\pi_i}$. It means that the dynamics on the boundary of Σ is determined by the four 3D Leslie-Gower maps $T|_{\pi_i}$, $i = 1, 2, 3, 4$.

Consider the general 3D Leslie-Gower model \hat{T} on \mathbb{R}_+^3 given by

$$\hat{T}_i(x) = \frac{(1 + r_i)x_i}{1 + \sum_{j=1}^3 r_i a_{ij} x_j}, \quad r_i, a_{ij} > 0, \quad i, j = 1, 2, 3. \quad (12)$$

Let $\hat{\Sigma}$ be the carrying simplex of \hat{T} . It is easy to see that there are three axial fixed points $v_{\{1\}}, v_{\{2\}}, v_{\{3\}}$ with $v_{\{i\}}$ lying on the positive x_i -axis, i.e.,

$$v_{\{1\}} = (\frac{1}{a_{11}}, 0, 0), v_{\{2\}} = (0, \frac{1}{a_{22}}, 0), \text{ and } v_{\{3\}} = (0, 0, \frac{1}{a_{33}}),$$

which are the vertices of the carrying simplex $\hat{\Sigma}$. There may exist a planar fixed point $s_{\{jk\}}$ lying on the positive cone of the $x_j x_k$ subspace, i.e. the interior of π_i , and there may also exist a positive fixed point p in \mathbb{R}_+^3 .

Set

$$\gamma_{ij} = a_{ii} - a_{ji}, \quad \beta_{ij} = \frac{a_{jj} - a_{ij}}{a_{ii}a_{jj} - a_{ij}a_{ji}}.$$

Lemmas 2 and 3 below follow from [9, Lemmas 4.5–4.7] immediately.

Lemma 2. *If $\gamma_{ij} > 0$ (resp. < 0) then $v_{\{i\}}$ repels (resp. attracts) along $\partial\Sigma \cap \pi_k$, and moreover, $v_{\{i\}}$ is hyperbolic if and only if $\gamma_{ij}\gamma_{ik} \neq 0$, where i, j, k are distinct.*

Lemma 3. *If $\gamma_{jk}\gamma_{kj} > 0$ then \hat{T} has a planar fixed point $s_{\{jk\}}$ in the interior of π_i , where i, j, k are distinct. Moreover, if $\gamma_{jk}, \gamma_{kj} < 0$ (resp. > 0) then $s_{\{jk\}}$ repels (resp. attracts) along $\partial\Sigma$; if $a_{ij}\beta_{jk} + a_{ik}\beta_{kj} < 1$ (resp. > 1) then $s_{\{jk\}}$ locally repels (resp. attracts) in $\hat{\Sigma}$; $s_{\{jk\}}$ is hyperbolic if and only if $a_{ij}\beta_{jk} + a_{ik}\beta_{kj} \neq 1$.*

Remark 3.1. *The biological meaning of the condition $\gamma_{ij} > 0$ (resp. < 0) is that species j can (resp. cannot) invade the monomorphic population of species i at the steady state $v_{\{i\}}$; here i, j are distinct. Suppose $s_{\{jk\}}$ exists which is a stable coexistence of species j and k in the absence of species i (for example, if $\gamma_{jk}, \gamma_{kj} > 0$ then $s_{\{jk\}}$ exists and it is stable in the interior of π_i). In this case, the biological meaning of the condition $a_{ij}\beta_{jk} + a_{ik}\beta_{kj} < 1$ (resp. > 1) is that the species i can (resp. cannot) invade the dimorphic population set by species j and k at the steady state $s_{\{jk\}}$; here i, j, k are distinct. A mathematical framework for treating questions of invasion and evolution that explicitly takes the population dynamics into account is adaptive dynamics; see [34, 35, 36, 37] for more details.*

Let S, \hat{S} be two 3D Leslie-Gower maps of type (12). S and \hat{S} are said to be equivalent relative to $\partial\hat{\Sigma}$ if there exists a permutation σ of $\{1, 2, 3\}$ such that S has an axial fixed point $v_{\{i\}}$ (resp. a planar fixed point $s_{\{jk\}}$) if and only if \hat{S} has an axial fixed point

$\hat{v}_{\{\sigma(i)\}}$ (resp. a planar fixed point $\hat{s}_{\{\sigma(j)\sigma(k)\}}$), and furthermore, $v_{\{i\}}$ (resp. $s_{\{jk\}}$) has
 the same hyperbolicity and local dynamics as $\hat{v}_{\{\sigma(i)\}}$ (resp. $\hat{s}_{\{\sigma(j)\sigma(k)\}}$). The map S is
 said to be stable relative to $\partial\hat{\Sigma}$ if all the fixed points on $\partial\hat{\Sigma}$ are hyperbolic. We say that
 an equivalence class is stable if each mapping in it is stable relative to $\partial\hat{\Sigma}$.

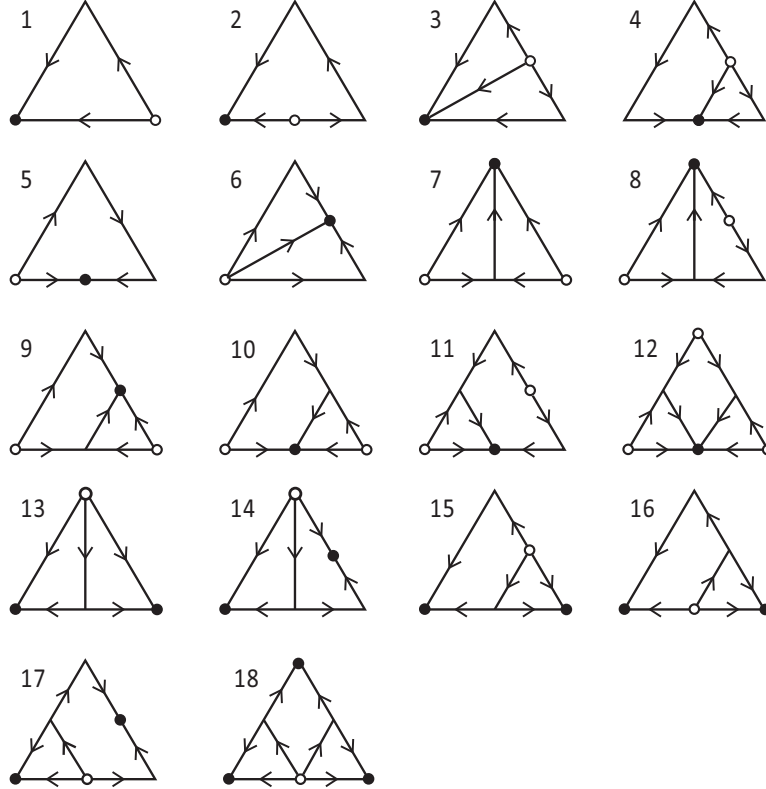


Figure 2: Carrying simplex dynamics in the equivalence classes 1 – 18 of the 3D Leslie-Gower model (12) with no positive fixed point. Redrawn from [9]. An attracting fixed point is denoted by a closed dot •, a repelling fixed point by an open dot ◦, and a saddle fixed point by the intersection of its stable and unstable manifolds.

Fig. 2 and Fig. 3 show the 33 stable equivalence classes via the boundary dynamics provided in [9]. In classes 1 – 25 and 33, only trivial dynamics can occur, that is every orbit converges to a fixed point [9, 13, 15, 38]. In class 33, there is a stable coexistence of the three species, while in classes 1 – 25, at least one species is driven to extinction. Neimark-Sacker bifurcations can occur in classes 26 – 31 but cannot occur in class 32, and in class 32 the positive fixed point is a repeller. In class 27, there is a heteroclinic

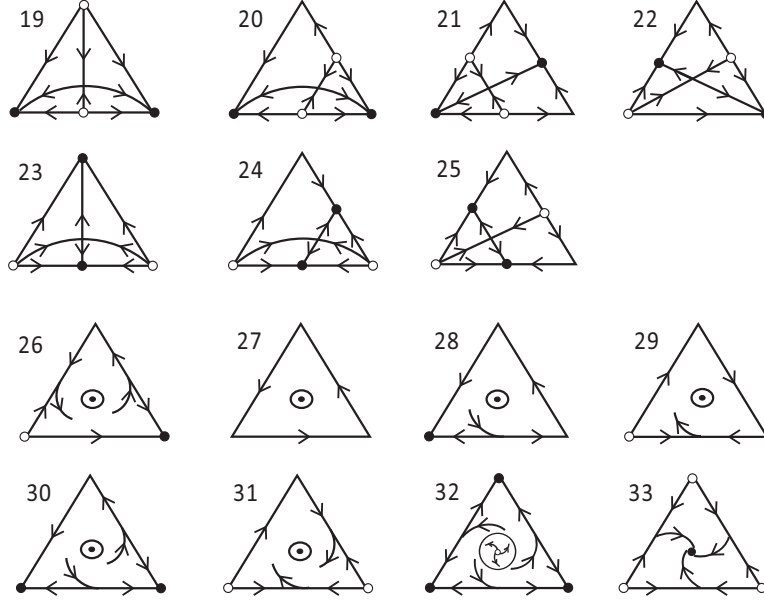


Figure 3: Carrying simplex dynamics in the equivalence classes 19 – 33 of the 3D Leslie-Gower model (12) with a positive fixed point. Redrawn from [9, 15, 38]. The fixed point notation is as in Fig. 2.

cycle which is the boundary of the carrying simplex. The symbol \odot in classes 26 – 31 represents a region of unknown dynamics. It means that the positive fixed point may be attracting, neutral or repelling on the carrying simplex and in a neighborhood of the positive fixed point, there may be invariant closed curves.

According to [9] and the above arguments, we specifically provide here the dynamics and the parameter conditions for the classes 4, 8, 9 and 27 of the 3D model (12) which will be used below to study the boundary dynamics of the 4D Leslie-Gower model (6).

Lemma 4. *The 3D Leslie-Gower map \hat{T} given by (12) is in the class 4 if there is a permutation σ of the indices $\{1, 2, 3\}$, after which \hat{T} satisfies*

- (i) $\gamma_{12} > 0, \gamma_{13} < 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$;
- (ii) $a_{12}\beta_{23} + a_{13}\beta_{32} < 1$;
- (iii) $a_{31}\beta_{12} + a_{32}\beta_{21} > 1$.

In this case, there are two planar fixed points $s_{\{12\}}, s_{\{23\}}$ and there is no positive fixed point. Moreover, $s_{\{12\}}$ is globally attracting on $\hat{\mathbb{R}}_+^3$. The phase portrait on $\hat{\Sigma}$ is shown in

Fig. 2-4, where the vertices can be interpreted as species 1: bottom left, species 2: bottom right, species 3: top.

Lemma 5. The 3D Leslie-Gower map \hat{T} given by (12) is in the class 8 if there is a permutation σ of the indices $\{1, 2, 3\}$, after which \hat{T} satisfies

$$(i) \quad \gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} < 0;$$

$$(ii) \quad a_{12}\beta_{23} + a_{13}\beta_{32} < 1;$$

$$(iii) \quad a_{31}\beta_{12} + a_{32}\beta_{21} < 1.$$

In this case, there are two planar fixed points $s_{\{12\}}, s_{\{23\}}$ and there is no positive fixed point. Moreover, $v_{\{3\}}$ is globally attracting on \mathbb{R}_+^3 . The phase portrait on $\hat{\Sigma}$ is shown in Fig. 2-8, where the vertices can be interpreted as species 1: bottom left, species 2: bottom right, species 3: top.

Lemma 6. The 3D Leslie-Gower map \hat{T} given by (12) is in the class 9 if there is a permutation σ of the indices $\{1, 2, 3\}$, after which \hat{T} satisfies

$$(i) \quad \gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0;$$

$$(ii) \quad a_{12}\beta_{23} + a_{13}\beta_{32} > 1;$$

$$(iii) \quad a_{31}\beta_{12} + a_{32}\beta_{21} < 1.$$

In this case, there are two planar fixed points $s_{\{12\}}, s_{\{23\}}$ and there is no positive fixed point. Moreover, $s_{\{23\}}$ is globally attracting on \mathbb{R}_+^3 . The phase portrait on $\hat{\Sigma}$ is shown in Fig. 2-9, where the vertices can be interpreted as species 1: bottom left, species 2: bottom right, species 3: top.

Lemma 7. The 3D Leslie-Gower map \hat{T} given by (12) is in the class 27 if there is a permutation σ of the indices $\{1, 2, 3\}$, after which \hat{T} satisfies

$$\gamma_{12} > 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} < 0.$$

In this case, there is a positive fixed point p and $\partial\hat{\Sigma}$ is a heteroclinic cycle. The phase portrait on $\hat{\Sigma}$ is shown in Fig. 3-27, where the vertices can be interpreted as species 1: bottom left, species 2: bottom right, species 3: top.

Set $\lambda_{ij} = \frac{(1+r_j)a_{ii}}{r_j a_{ji} + a_{ii}}$, where $i \neq j$. Let

$$\vartheta = \ln \lambda_{12} \ln \lambda_{23} \ln \lambda_{31} + \ln \lambda_{21} \ln \lambda_{13} \ln \lambda_{32}.$$

189

190 **Lemma 8** ([8]; see also [9]). *Assume the 3D Leslie-Gower map \hat{T} is in class 27. If*
 191 *$\vartheta > 0$ (resp. < 0), then the heteroclinic cycle $\partial\hat{\Sigma}$ of \hat{T} is repelling (resp. attracting).*

192 4. Dynamics analysis

In this section, we will study the dynamics on the carrying simplex for the 4D Leslie-Gower model T given by (6) with parameters r_i and a_{ij} given in (7) and (8) respectively. The fixed points of the 4D Leslie-Gower model T given by (6) are determined by the linear equations

$$x_i = 0 \quad \text{or} \quad \sum_{j=1}^4 a_{ij} x_j = 1, \quad i = 1, 2, 3, 4,$$

193 which depend only on the parameters a_{ij} . Therefore, the fixed points of T are indepen-
 194 dent of the parameter μ when the parameters r_i and a_{ij} are given in (7) and (8). That
 195 is to say, the values of the fixed points do not change as μ varies. It is easy to see that
 196 T has nine boundary fixed points:

- 197 • the trivial fixed point 0;
- 198 • four axial fixed points $v_{\{1\}}, v_{\{2\}}, v_{\{3\}}, v_{\{4\}}$ with $v_{\{i\}}$ lying on positive x_i -axis;
- 199 • three planar fixed points $s_{\{12\}}, s_{\{23\}}, s_{\{24\}}$ with $s_{\{ij\}}$ lying on the positive cone of
 200 the $x_i x_j$ subspace;
- 201 • a fixed point $q^{\{2\}} \approx (0.1046, 0, 0.1946, 0.0746)^\tau$ on the positive cone of the $x_1 x_3 x_4$
 202 subspace,

and a unique positive fixed point p with

$$p \approx (0.08734, 0.06352, 0.1333, 0.1024)^\tau.$$

203 T admits a 3D carrying simplex Σ homeomorphic to Δ^3 ; see Fig. 4. All the nontrivial
 204 boundary fixed points lie on $\partial\Sigma$ and p lies in $\dot{\Sigma}$. It is easy to check that all the nine
 205 boundary fixed points are unstable for all $\mu > 0$ by their Jacobian matrices.

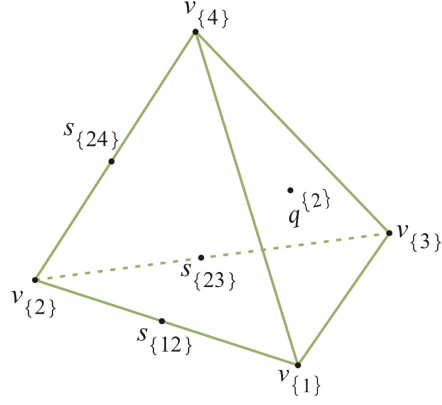


Figure 4: Carrying simplex for the Leslie-Gower map T given by (6). A fixed point on the boundary is represented by a closed dot \bullet .

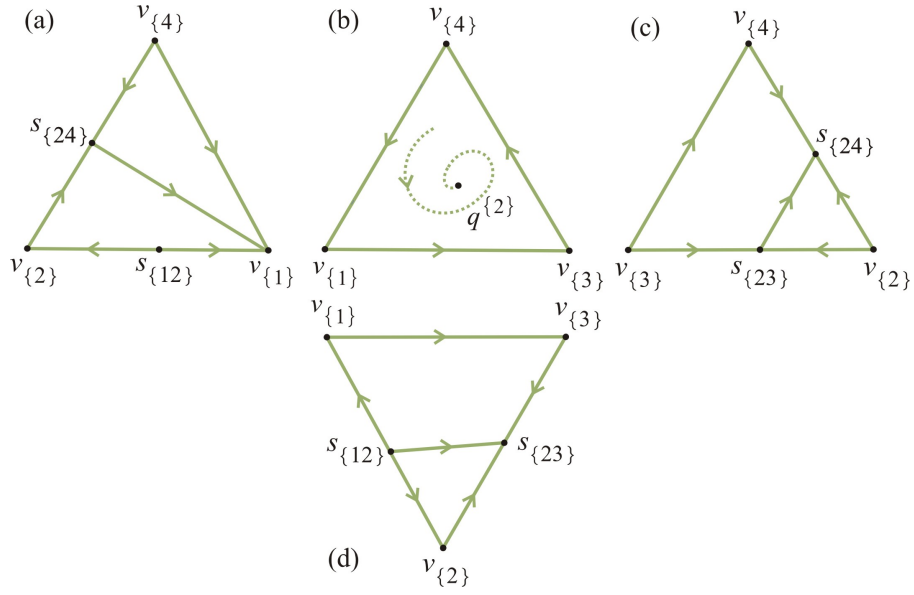


Figure 5: The phase portrait on $\partial\Sigma$ for the Leslie-Gower map T given by (6). (a) The phase portrait on $(\partial\Sigma)_3$. (b) The phase portrait on $(\partial\Sigma)_2$. (c) The phase portrait on $(\partial\Sigma)_1$. (d) The phase portrait on $(\partial\Sigma)_4$.

4.1. Boundary dynamics

Recall that each coordinate plane π_i is positively invariant under T , and $T|_{\pi_i}$ is a 3D Leslie-Gower model which admits a 2D carrying simplex. Moreover, $\partial\Sigma$ is composed of the 2D carrying simplices of $T|_{\pi_i}$, $i = 1, 2, 3, 4$.

By Lemmas 4–7 it is easy to check that $T|_{\pi_4}$ is in class 4 (see Fig. 5(d)), $T|_{\pi_3}$ is in class 8 (see Fig. 5(a)), $T|_{\pi_2}$ is in class 27 (see Fig. 5(b)), and $T|_{\pi_1}$ is in class 9 (see Fig. 5(c)) for all $\mu > 0$. It then follows that $s_{\{23\}}$ is globally attracting on the interior of π_4 for $T|_{\pi_4}$, $v_{\{1\}}$ is globally attracting on the interior of π_3 for $T|_{\pi_3}$, and $s_{\{24\}}$ is globally attracting on the interior of π_1 for $T|_{\pi_1}$. Therefore, the global dynamics is known for $T|_{\pi_4}$, $T|_{\pi_3}$ and $T|_{\pi_1}$, and every nontrivial orbit converges to some boundary fixed point, which is independent of μ . Since $T|_{\pi_2}$ is in class 27, the three edges of $(\partial\Sigma)_2$ form a heteroclinic cycle and there is a fixed point (i.e. $q^{\{2\}}$) in the interior of $(\partial\Sigma)_2$; see Fig. 5(b). The heteroclinic cycle is repelling for $T|_{\pi_2}$ by Lemma 8. The Jacobian matrix $DT|_{\pi_2}(q^{\{2\}})$ has eigenvalues $0.8562, 0.9901 \pm 0.0395i$, which are the three internal eigenvalues of $DT(q^{\{2\}})$. Thus, $q^{\{2\}}$ is stable for $T|_{\pi_2}$. Note that $T|_{\pi_2}$ is independent of μ , so the boundary dynamics of T is independent of μ , and the dynamics on $\partial\Sigma$ for T is shown in Fig. 5. On the other hand, the external eigenvalue of $DT(q^{\{2\}})$ is $\frac{1+\mu}{1+0.9013\mu} > 1$, so $q^{\{2\}}$ is unstable for T when $\mu > 0$. Therefore, we conclude that the dynamics on the boundary of the carrying simplex which is shown in Fig. 5 and the stability of the fixed points on the boundary of the carrying simplex do not change as the parameter μ varies.

4.2. Evolution of the interior attractor

In this subsection, we study the evolution of the attractor within $\dot{\Sigma}$ for increasing μ from zero. We find that chaotic attractors can occur in $\dot{\Sigma}$, and the route to chaos was detected as the parameter μ is increased. Specifically, in this model

- cascades of quasiperiod-doubling bifurcations can occur which lead to chaos eventually.

Quasiperiod-doubling bifurcation in our context is referred to the phenomenon that a quasiperiodic curve rounding twice bifurcates from the original one. We call the bifurcated quasiperiodic curve a 2-quasiperiodic curve. The similar phenomena have also been observed in [39, 40].

At $\mu \approx 0.1537$, the positive fixed point undergoes a supercritical Neimark-Sacker bifurcation with first Lyapunov coefficient $L_1(0) = -0.6667 < 0$ (see [41, 42]). The fixed point becomes unstable and a stable invariant cycle can occur for $\mu > 0.1537$. Fig. 6(a) shows the attracting quasiperiodic curve when $\mu = 0.2$. As μ is increased from 0.2

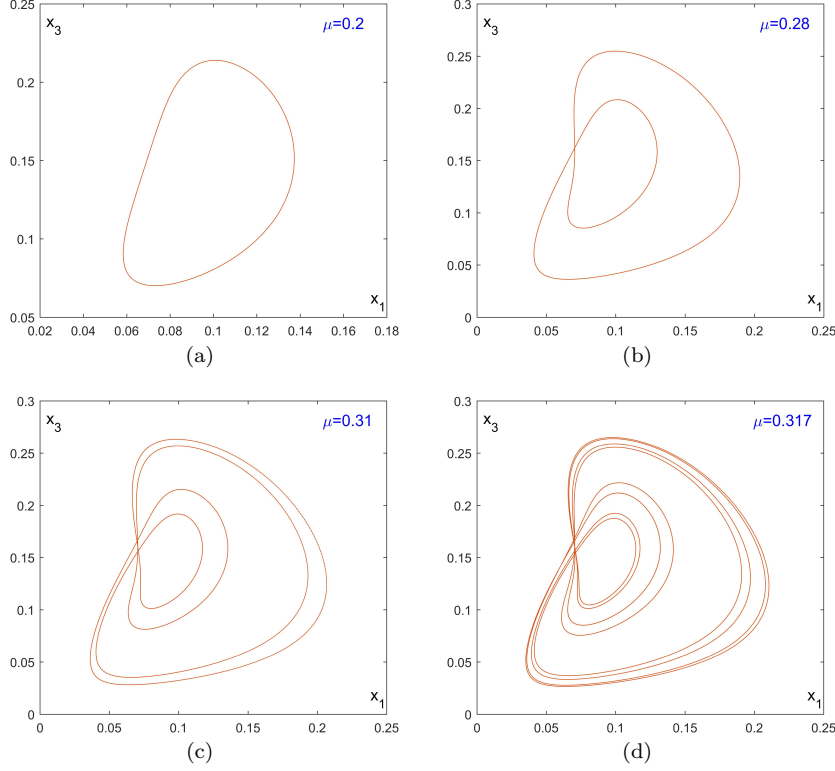


Figure 6: Evolution of the interior attractor as μ is increased from 0.2 to 0.317. (a) The attractor at $\mu = 0.2$ is a quasiperiodic curve. (b) The attractor at $\mu = 0.28$ is a 2-quasiperiodic curve. (c) The attractor at $\mu = 0.31$ is a 4-quasiperiodic curve. (d) The attractor at $\mu = 0.317$ is a 8-quasiperiodic curve.

the quasiperiodic curve increases in size, until about $\mu = 0.246$, where a quasiperiod-doubling cascade begins; Figs. 6(b)–6(d) show the attracting 2-quasiperiodic curve, 4-quasiperiodic curve and 8-quasiperiodic curve at $\mu = 0.28$, $\mu = 0.31$ and $\mu = 0.317$, respectively. Such quasiperiod-doubling cascades eventually lead to chaos at about $\mu = 0.3185$. Figs. 7(a)–7(f) show the different chaotic attractors for different values of the parameter $\mu > 0.3185$.

The corresponding Lyapunov exponents as functions of μ are shown in Fig. 8, from which we can see that the largest Lyapunov exponent is positive for some $0.318 < \mu < 0.494$, such as the values of μ in Fig. 7, which indicates the presence of chaotic attractors. Note that as μ is increased from 0.318, there also exist some regions such that the largest

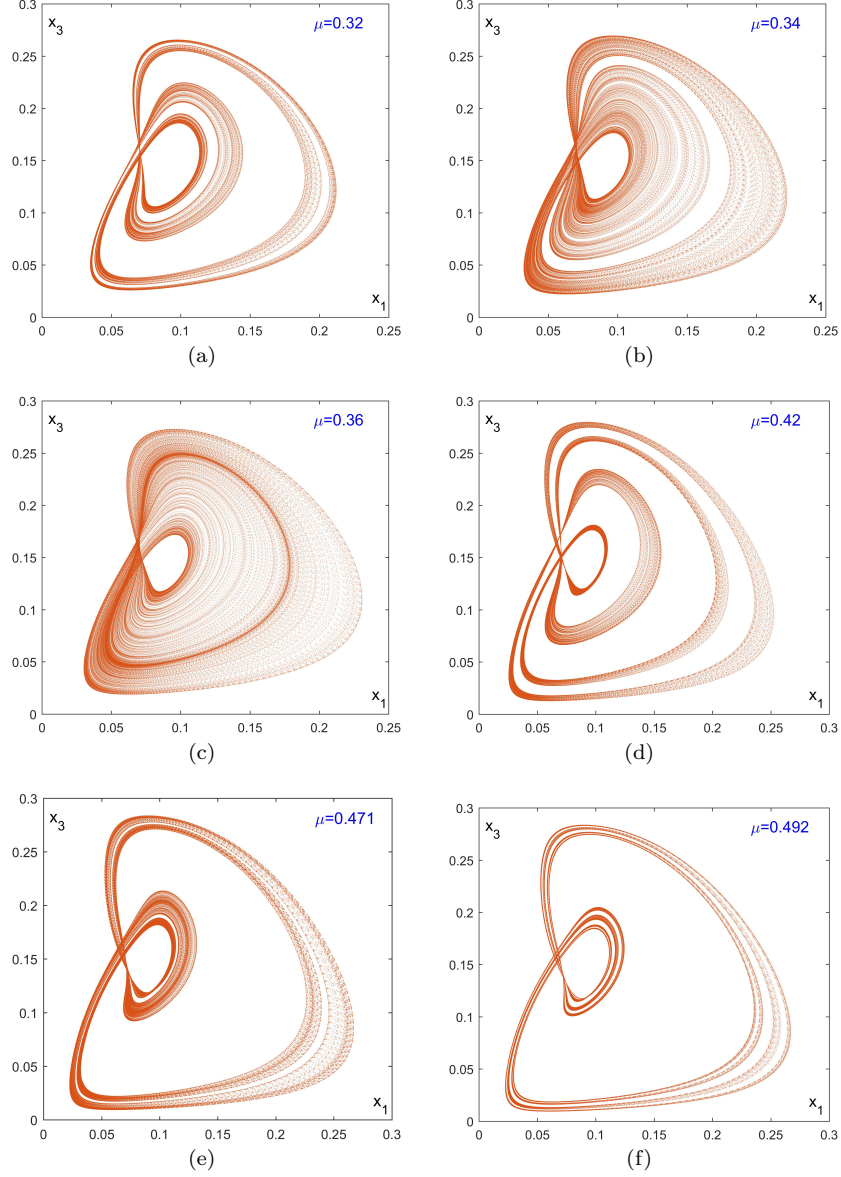


Figure 7: Evolution of the interior attractor as μ is increased from 0.32 to 0.492. (a) The chaotic attractor for $\mu = 0.32$. (b) The chaotic attractor for $\mu = 0.34$. (c) The chaotic attractor for $\mu = 0.36$. (d) The chaotic attractor for $\mu = 0.42$. (e) The chaotic attractor for $\mu = 0.471$. (f) The chaotic attractor for $\mu = 0.492$. The successive iterates T^k of T have been applied to the initial point $x^{[0]} = (0.1046, 0.01, 0.1946, 0.0746)^T$ for each μ , producing a sequence asymptotic to the chaotic attractor. Here, 200000 points of this sequence are plotted, ignoring the first 50000 iterates.

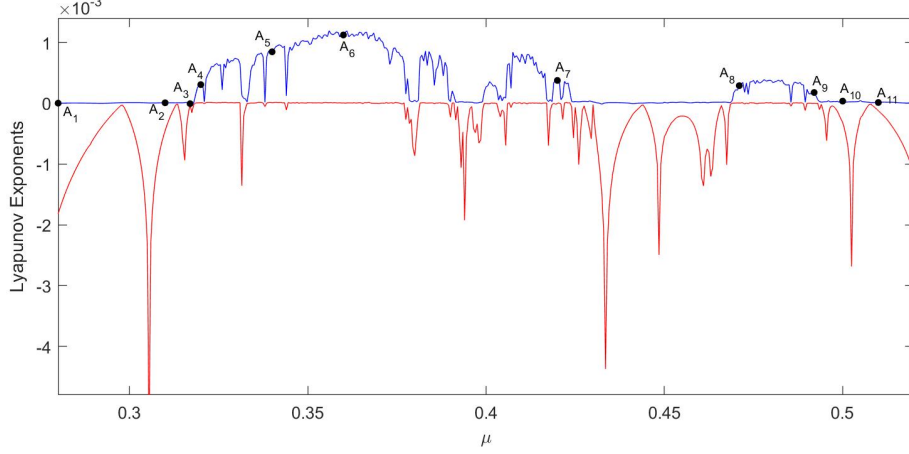


Figure 8: The corresponding largest (blue curve) and the second largest (red curve) Lyapunov exponents as functions of $\mu \in [0.28, 0.52]$. The parameter values μ used in Figs 6, 7, 9 with the corresponding largest Lyapunov exponents are marked with the closed dots \bullet , where $A_1 = (0.28, 0)$, $A_2 = (0.31, 0)$, $A_3 = (0.317, 0)$, $A_4 = (0.32, 0.0003)$, $A_5 = (0.34, 0.0008)$, $A_6 = (0.36, 0.0011)$, $A_7 = (0.42, 0.0004)$, $A_8 = (0.471, 0.0003)$, $A_9 = (0.492, 0.0002)$, $A_{10} = (0.5, 0)$, and $A_{11} = (0.51, 0)$. The largest Lyapunov exponents are 0 for $\mu = 0.2, 0.8, 1$, which are not plotted in the figure.

Lyapunov exponent is zero, which are the quasiperiodic windows, i.e., quasiperiodic curves appear again for these values of μ . However, when $\mu > 0.494$ the chaotic attractor disappears and an inverse quasiperiod-doubling cascade begins; see Figs. 9(a)–9(d).

Remark 4.1. One can also let another parameter change to observe the evolution of the interior attractor once a chaotic attractor is found. For example, by setting $\mu = 0.36$ and fixing all r_i and a_{ij} given in (7) and (8) except r_1 , one can find the similar bifurcation scenarios and the evolution of the interior attractor when r_1 is increased from 0 to 0.4.

4.3. Invasion can lead to chaos

Consider the subsystem $T|_{\pi_2}$ of species 1, 3 and 4 given by

$$\begin{cases} T_1(x) = \frac{(1+r_1)x_1}{1+r_1(a_{11}x_1+a_{13}x_3+a_{14}x_4)} \\ T_3(x) = \frac{(1+r_3)x_3}{1+r_3(a_{31}x_1+a_{33}x_3+a_{34}x_4)} \\ T_4(x) = \frac{(1+r_4)x_4}{1+r_4(a_{41}x_1+a_{43}x_3+a_{44}x_4)} \end{cases} \quad (13)$$

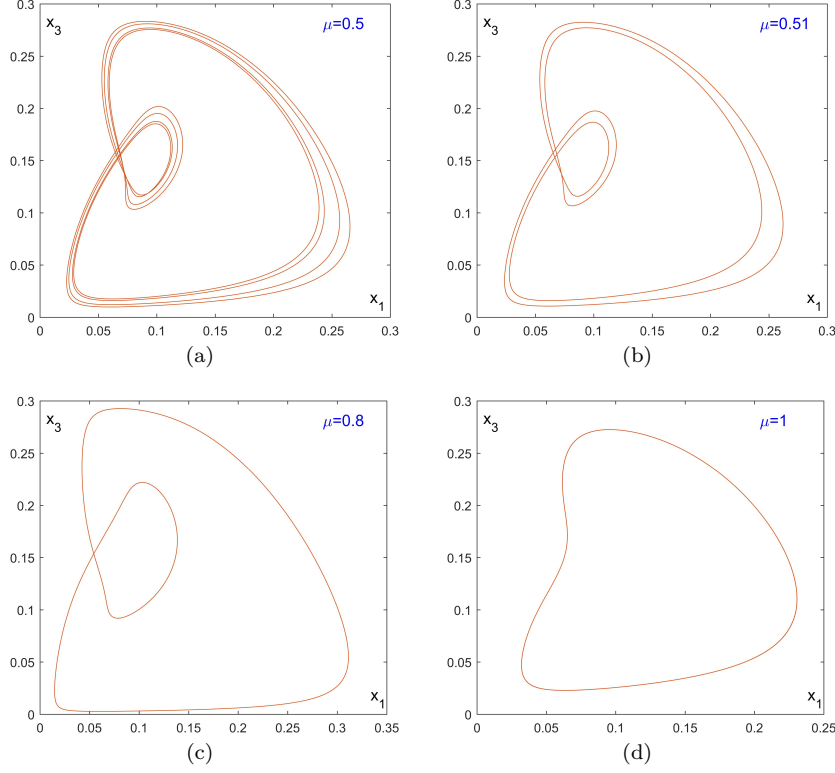


Figure 9: Evolution of the interior attractor as μ is increased from 0.5 to 1. (a) The attractor at $\mu = 0.5$ is a 8-quasiperiodic curve. (b) The attractor at $\mu = 0.51$ is a 4-quasiperiodic curve. (c) The attractor at $\mu = 0.8$ is a 2-quasiperiodic curve. (d) The attractor at $\mu = 1$ is a quasiperiodic curve.

with r_i, a_{ij} given in (7) and (8), $i, j = 1, 3, 4$. Recall that $T|_{\pi_2}$ is in the class 27, so the axial fixed point $v_{\{1\}}$ is stable in the x_1x_4 subspace and unstable in the x_1x_3 subspace, the axial fixed point $v_{\{3\}}$ is stable in the x_1x_3 subspace and unstable in the x_3x_4 subspace, and the axial fixed point $v_{\{4\}}$ is stable in the x_3x_4 subspace and unstable in the x_1x_4 subspace. In particular, the boundary of $(\partial\Sigma)_2$ is a heteroclinic cycle (see Fig. 5(b)), which is due to the competition relations

$$\begin{aligned} a_{11} &> a_{31}, \quad a_{13} > a_{33}, \\ a_{33} &> a_{43}, \quad a_{34} > a_{44}, \\ a_{41} &> a_{11}, \quad a_{44} > a_{14}. \end{aligned} \tag{14}$$

In adaptive dynamics, the relations in (14) mean that the species 3 can invade species 1 (in the absence of species 4) but not vice versa, and the outcome is that species 1 is

267 driven to extinction, whilst species 3 remains extant; the species 4 can invade species 3
 268 (in the absence of species 1) but not vice versa, and the outcome is that species 3 is driven
 269 to extinction, whilst species 4 remains extant; the species 1 can invade species 4 (in the
 270 absence of species 3) but not vice versa, and the outcome is that species 4 is driven to ex-
 271 tinction, whilst species 1 remains extant; see Remark 3.1. This means that the species 1,
 272 3 and 4 compete in the rock-paper-scissors manner under the Leslie-Gower dynamics de-
 273 scribed by $T|_{\pi_2}$. However, there is a stable fixed point $q^{\{2\}} \approx (0.1046, 0, 0.1946, 0.0746)^\tau$
 274 for $T|_{\pi_2}$, so the species 1, 3 and 4 can coexist at the stable steady state $q^{\{2\}}$.

275 The outcomes of invasion attempts by an invader (i.e. species 2) into the trimorphic
 276 resident population set by species 1, 3 and 4 at the steady state $q^{\{2\}}$ are of particular
 277 interest. To begin with, the trimorphic resident population is at the steady state $q^{\{2\}}$
 278 and then the invader species 2 is introduced in small quantities. Since the external
 279 eigenvalue of $DT(q^{\{2\}})$ is $\frac{1+\mu}{1+0.9013\mu} > 1$, which implies the invasion fitness of species 2 in
 280 an environment set by species 1, 3 and 4 at the steady state $q^{\{2\}}$ given by $\ln \frac{1+\mu}{1+0.9013\mu}$
 281 is positive for all $\mu > 0$, the species 2 can always successfully invade such a trimorphic
 282 resident population. Moreover, since $T|_{\pi_2}$ is independent of μ , the environment set by
 283 the resident species 1, 3 and 4 at the steady state $q^{\{2\}}$ is independent of μ . This allows
 284 one to study the possible outcomes of invasion attempts by the invader species 2 into
 285 such a fixed environment for different values of μ .

286 Our results in section 4.2 show that the outcomes of the invasion attempts by the
 287 species 2 will be different as the change of the parameter μ . For example, for $\mu < 0.1537$,
 288 the Leslie-Gower model T given by (6) of the four competing species has a stable positive
 289 fixed point p which means a coexistence steady state of the invader species 2 and the
 290 resident species 1, 3 and 4; for $\mu = 0.2$, the model T has an attracting quasiperiodic curve,
 291 which means a quasiperiodic coexistence of the invader species 2 and the resident species
 292 1, 3 and 4; for $\mu = 0.36$, the model T has a chaotic attractor which means a chaotic
 293 coexistence of the invader species 2 and the resident species 1, 3 and 4. Importantly,
 294 our results show that the invasion by an invader into a trimorphic population under the
 295 Leslie-Gower dynamics can lead to chaos.

296 5. Discussion

297 This paper presents a case study of chaos in the classical Leslie-Gower model of four
 298 competing species induced by the map (6). The selection of parameters is based on a
 299 brute-force numerical search in the parameter space consisting of r_i and a_{ij} such that
 300 the largest Lyapunov exponent of the orbit with the given initial value is positive. The
 301 numerical result shows that the largest Lyapunov exponent is positive when r_i and a_{ij}
 302 are equal to the values in (7) and (8) with $\mu = 0.32$, which implies the occurrence of
 303 chaos. We then explore the mechanism of occurrence of chaos in the 4D Leslie-Gower
 304 map, especially the route to chaos. To begin with, we choose the parameters r_i, a_{ij} given
 305 in (7) and (8) with $\mu = 0.32$ such that the 4D Leslie-Gower map has a chaotic attractor.
 306 We notice that species 1, 3 and 4 competing in the rock-paper-scissors manner can coexist
 307 in a stable steady state $q^{\{2\}}$ which is independent of the parameter μ , so we then fix all
 308 r_i, a_{ij} in (7) and (8) except μ . By selecting such parameters, in addition to observing
 309 the evolution of the interior attractor, one can observe the possible outcomes of invasion
 310 attempts by the invader species 2 into a fixed environment set by the resident species 1,
 311 3 and 4 at the steady state $q^{\{2\}}$ as μ varies.

312 A quasiperiod-doubling route to chaos is found in the 4D Leslie-Gower map (6) as μ is
 313 increased from 0 to 1. Specifically, increasing μ from 0, the map undergoes a supercritical
 314 Neimark-Sacker bifurcation, which bifurcates a stable quasiperiodic curve, and then the
 315 map undergoes a cascade of quasiperiod-doubling bifurcations, and after a critical point
 316 becomes chaotic, as illustrated in Fig. 6 and Fig. 7. Biologically, the results indicate
 317 a possible outcome of invasion attempts by an invader (species 2) into the environment
 318 set by the resident species 1, 3 and 4 at a steady state which compete in the rock-paper-
 319 scissors manner under the Leslie-Gower dynamics, that is the invasion can lead to chaos.
 320 However, the outcomes of the invasion might be different as the parameter μ varies, that
 321 is the invasion may lead to quasiperiodic behavior or chaotic behavior which depends on
 322 the value of the parameter μ ; see Figs. 6–9.

323 Since the 4D Leslie-Gower map has a 3D carrying simplex Σ , the chaotic attractor is
 324 contained in the interior of this invariant manifold. This means that the 4D Leslie-Gower
 325 map can admit a 3D carrying simplex containing a chaotic attractor. In order to have
 326 a clearer understanding of the dynamics on the carrying simplex, we further study the

dynamics on the boundary of the carrying simplex in detail. The study shows that the boundary dynamics which is independent of the parameter μ is determined by the classes 4, 8, 9 and 27 provided by Jiang and Niu in [9] for the 3D Leslie-Gower map. The phase portrait on the boundary of the carrying simplex is shown in Fig. 5. Therefore, in the 4D Leslie-Gower map (6), as μ is increased from 0, the interior attractor evolves from a fixed point to a quasiperiodic curve, and then from a quasiperiodic curve to a chaotic attractor, but the boundary dynamics remains unchanged.

Recall that the carrying simplex Σ carries all the asymptotic dynamics, and the 4D Leslie-Gower competitive map restricted to Σ is a 3D homeomorphism, so the 4D Leslie-Gower map actually behaves like a 3D homeomorphism. On the other hand, for the 1D and 2D Leslie-Gower maps, every orbit converges to a fixed point, so there is no chaos. The 3D Leslie-Gower map which behaves like a 2D homeomorphism was classified into 33 stable equivalence classes via the boundary dynamics on the carrying simplex in [9], and it was proved that every orbit converges to a fixed point and hence chaos cannot occur in classes 1 – 25 and 33 ([9, 13, 15]). In classes 26 – 31, Neimark-Sacker bifurcations can occur which cannot occur in class 32. However, the 3D Leslie-Gower map (2) presents the similar dynamic scenarios as the 3D Lotka-Volterra competition model (5) [18, 19] in which chaos cannot occur due to the carrying simplex theory [1, 43] and the Poincaré-Bendixson theorem. Moreover, we have carried out a brute-force numerical search in the 3D Leslie-Gower map but no chaotic attractor has been observed. Therefore, by the numerical experiment and the comparison between the 3D Leslie-Gower map (2) and the 3D Lotka-Volterra competition model (5), we conjecture that chaos may not occur in the 3D Leslie-Gower map and the 4D Leslie-Gower map is probably the simplest example that might have chaos.

Note that the Poincaré-Bendixson theorem does not hold for discrete-time dynamical systems. To the best of our knowledge, the available results on nonexistence of chaos for 3D competitive maps with a carrying simplex are the following: Ruiz-Herrera [6] proved that every orbit converges to a fixed point when there is no positive fixed point; Niu and Ruiz-Herrera [13] proved that every orbit converges to a fixed point when there is a unique positive fixed point whose index is -1 ; Balreira, Elaydi and Luís [14] and Gyllenberg, Jiang and Niu [15] provided criteria on the global stability of the unique

positive fixed point under special conditions. However, it should be pointed out that how to prove there is no chaos in the 3D Leslie-Gower competitive map is still a very difficult problem, which is left for future research.

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